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Inhibition and blocking with temporal cues in conditioned suppression of barpressing.

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INHIBITION AND BLOCKING WITH TEMPORAL CUES IN CONDITIONED SUPPRESSION OF BARPRESSING

A Dissertation Presented

By

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ABSTRACT

Inhibition and Blocking with Temporal Cues in Conditioned Suppression of Barpressing

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The role of temporal cues in inhibition and blocking was explored in three experiments using rats in a conditioned suppression procedure. In Experiments 1 and 2 a retardation and a summation test demonstrated that the temporal cues during shock-free periods following shock control inhibitory strength. Experiment 3 found no evidence for blocking of excitation to discrete cues by temporal cues that had preceded shock or for blocking of inhibition to discrete cues by temporal cues that had followed shock. The failure to obtain blocking with temporal cues was attributed to factors known to be important in obtaining blocking with discrete cues. The results of the experiments suggest that the functional nature of temporal cues in inhibition and blocking is consistent with empirical findings and theoretical descriptions of the nature of discrete cues.

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The purpose of the research described below is to examine the functional nature of time as a stimulus in Pavlovian fear conditioning. Specifically the research is an attempt to describe the role of temporal cues using a conditioned suppression procedure in which grid shock unconditioned stimuli (USs) are administered to rats while they are barpressing for sucrose on a variable interval (VI) schedule of reinforcement.

There is substantial evidence that temporal cues in a variety of procedures (i.e. temporal conditioning, Pavlov, 1927; delayed conditioning, Pavlov, 1927; fixed interval schedules, Skinner, 1938; unsignalled avoidance, Sidman, 1953; differential reinforcement of low rate schedules, Anger, 1956) can come to control an animal's responding. The nature of temporal cues and their relation to other cues is, however, not well understood. Several hypotheses of how an animal's behavior is controlled by time have been advanced. Most of these hypotheses attempt to point out some event or sequence of events which the animal is assumed to have access to. Bruner and Revusky (1961), for example, propose that an animal mediates time intervals by engaging in some overt chain of behaviors. Another proposal is that an animal learns to respond differentially to temporal changes in proprioceptive feedback from some previous response or stimulus (Hull, 1943). Other explanations appeal to correlations between internal mechanisms and time. Holubar (1969), for example, suggests that EEG rhythms are basic timing mechanisms. In the research described below no attempt is made to find empirical support for one hypothesis or another. It is assumed only that a rat does have access to some events, internal or external, that allows the rat's behavior to be controlled by temporal cues.

Although there have been several Russian studies of temporal conditioning (Dmitriev & Kochiniga, 1959) there have been few American studies. The Russian studies cited by Dmitriev & Kochiniga are of limited value since they are not readily available in translation and because they use procedures which differ greatly from contemporary procedures making it difficult to evaluate their results in terms of present day theoretical views and methodological criteria. The paucity of American studies of temporal conditioning has probably occurred partly because of some recent failures to demonstrate temporal conditioning (cf. Lockhart, 1966) although there have been some successes (Imada & Okamura, 1975; LaBarbera & Church, 1974; Lockhart, 1966) and partly because some of the more recent formulations of classical conditioning (Kamin, 1969; Rescorla & Wagner, 1972) do not formally deal with temporal cues.

Rescorla and Wagner (1972) have advanced a model of the classical conditioning process that can account for many classical conditioning phenomena (Rescorla, 1972). The model is a linear model in which the change in the associative strength of a stimulus on a particular trial is a function of the difference between the asymptotic level of conditioning obtainable with the US used and the current associative strength of all stimuli present. Formally, the change in associative strength to stimulus X, (ΔV_X) is given by,

$$\Delta V_x = \alpha \beta (\lambda - V_{AX})$$

where α depends on the salience of X; β is a learning rate parameter dependent on the US used; λ is the asymptotic level of conditioning obtainable; and V_{AX} is the sum of the associative strengths of the stimuli present (i.e., $V_{AX}=V_A+V_X$).

Despite the model's success in describing the results of many experimental manipulations, the model cannot readily deal with the effects of temporal variables. Rescorla (1972) acknowledges this and suggests that when more is known about the role of temporal variables in Pavlovian conditioning, the model could be extended to account for these variables. The problem with the model in its present form is that conditioned stimuli (CSs) are assumed to be discrete events that are invariant in their control over a particular period of time (typically the trial length which is set equal to the CS duration). But temporal cues by definition are not discrete and vary with time. Thus to the extent that an animal can be controlled differentially by temporal cues within a particular period, the model incorrectly describes behavior as invariant during that period.

Much of the impetus for the research below grew out of an attempted explanation of the result of an experiment by Ayres, Mahoney, Proulx, & Benedict (1976; Experiment 2). Therefore, the experiment and the results will be described in detail.

In the experiment, rats received Pavlovian forward defense conditioning in which tonal CSs terminated in the onset of scrambled grid shock USs. Following this experience, the rats then received in the conditioning chambers either of five treatments: presentations of (1) CSs alone (CSa), (2) USs alone (USa), (3) backward pairings of CSs and USs (Bck), (4) independently and randomly distributed CSs and USs (TR), or (5) no stimuli (No-Ext). Finally all rats were tested for suppression to the tone alone. During all phases of the experiment the rats were able to barpress for sucrose on a VI 2-min schedule of reinforcement. Suppression ratios for each animal were formed by dividing the number of responses made during a CS presentation by the total number of responses made during that CS and an equivalent time period before the CS. For the US-alone group, the time after the US was used as a "dummy" CS period in the ratio. The results of the experiment are shown in Figure 1. The groups did not differ during forward conditioning (panel A) but did differ during the experimental treatment phase (panel B). Group USa showed little suppression to the dummy CS from the very first trial. Group Bck showed less suppression than it had during forward conditioning (apparent extinction) but more suppression than Group USa. Groups CSa and TR, on the other hand, showed only a gradual extinction effect over trials. During the subsequent CS-alone test phase (panel C), however, there was a shift in the rank ordering of the groups. Group USa and No-Ext showed significantly less suppression but did not differ reliably from each other; and Group CSa showed the least suppression.

Thus although it appeared from the experimental phase that backward pairings had led to the extinction of the excitatory CS, the test phase did not support this. Burdick and James (1973) found a similar effect, but their procedure did not allow them to distinguish between several possible explanations of this apparent extinction. Ayres et al. were, however, able to suggest an explanation based on the performance of the USa group. They proposed that during forward conditioning, the temporal stimuli following the US acquired inhibitory strength because these stimuli were never closely followed by the next US (The intertrial interval had ranged from 7 to 19 min.). Therefore the reduced suppression to the post-shock CS in Group Bck during extinction really represented suppression to the compound of the excitatory CS and the inhibitory post-shock temporal stimuli. Assuming algebraic summation of excitatory and inhibitory tendencies, the suppression to the compound should be less than that to the CS alone. Thus when the CS was presented alone in the final phase (panel C), it should still control strong suppression despite the apparent extinction. Support for this explanation came from comparisons between groups. During the treatment phase, suppression to the CS in Group Bck was greater than suppression in Group USa and less than suppression to the CS in Group CSa, indicating that the suppression to the CS in Group Bck represented strong suppression to the CS diminished by the inhibitory strength of the post-US temporal cues.

The finding of reduced suppression following shock in the Ayres et al. study was not new. The effect was found early in conditioned suppression research (Estes & Skinner, 1941), and a variety of explanations of the phenomenon have been advanced. Weiss and Strongman (1969) proposed that the accelerated responding was shock-elicited and might possibly represent aggression to the bar. Church and Getty (1972) demonstrated how without proper controls a rat merely reacting to shock may appear to be anticipating that event. They suggested that shock-elicited responding may be due to some stereotyped response, or species specific defense reaction, or disinhibition of responding. LaBarbera and Caul (1976) found postshock bursts of responding consistent with predictions from the opponent-process theory of motivation (Solomon & Corbit, 1975). They suggested that repeated shock presentations intensify a postulated positive afterreaction to an aversive event. This positive afterreaction would presumably be reflected by decreased suppression following shock. Finally, the postshock responding could be due, as suggested by Ayres et al., to the acquisition of inhibitory strength to the post-US period. Davis and McIntire (1969) also proposed that post-shock bursts of responding were due to inhibition. They suggested that inhibition would occur because the US (with a sufficiently long intershock interval) signals a shock-free interval. Davis and his colleagues have subsequently referred to the contingency (if shock then no shock) involved in this procedure as "second order contingencies" (Davis, 1970) or "autocontingencies" (Davis, Memmott, and Hurwitz, 1975). It has already been demonstrated that with a discrete post-shock CS, the CS becomes inhibitory (Moscovitch & LoLordo, 1968; Siegel & Domjan, 1971, 1974). The Ayres et al. experiment did demonstrate that less excitation was associated with the time after shock than was associated with a pre-CS period, but it did not demonstrate that the post-shock time was inhibitory. In Experiment 1 an attempt was made to demonstrate that the time after shock is indeed inhibitory.

Experiment 1

Rescorla (1969) has suggested that in order to demonstrate the inhibitory nature of a CS, two tests should be used; a retardation test and a summation test. In the retardation test the CS is paired with a US and the rate of acquisition of a CR to that CS is compared with the rate of acquisition of a CR to a CS in a control group which did not have the inhibitory training. Presumably the inhibitory CS will acquire excitatory strength more slowly than the neutral CS of the control group. In a summation test the presumed inhibitory CS is given in compound with a known excitor. If the CS is indeed inhibitory, then the strength of the response to the compound should be reduced relative to the strength of the response to the excitatory CS alone. The summation test is needed in addition to the retardation test because slow acquisition in the retardation test could be due to reduced salience of the presumed inhibitory CS. A summation test rules out the reduced salience hypothesis because the stimulus in question cannot have an effect in the summation test unless the subject attends to it. The retardation test is needed in addition to the summation test because the weakened CR to the compound compared to the CR to the excitatory CS alone may be due to a relatively strong salience of the presumed inhibitor. This interpretation is ruled out by the retardation test, because if the stimulus is so salient as to distract the subject's attention from the excitor, then retarded acquisition to that stimulus must be due to its inhibitory properties and not to a failure to attend to it.

There is some evidence in the Ayres et al. experiment that indicates that a summation test would show that the time after shock is inhibitory. In that study, Group Bck received forward conditioning trials and then received backward pairings of the CS and US. Group CSa received forward conditioning trials and then received

CS-alone trials. The results showed that suppression to the CS-alone in Group CSa was greater than suppression to the CS plus time after shock in Group Bck. Although these results are the ones sought in a summation test, they do not represent strong evidence. The Ayres et al. study contained no procedure to control for stimulus generalization decrement. A reduction in suppression to the compound (CS plus time after shock) relative to the excitor (the CS) alone could be expected on the basis of generalization decrement alone.

In Experiment 1 a summation and a retardation test were run to demonstrate that time after shock is inhibitory. In the experimental groups, in an attempt to make time after shock inhibitory, shocks were presented with a constant intershock interval. In the control groups shocks were presented with a variable intershock interval that was designed (Fleshler & Hoffman, 1962) to make the occurrence of a shock equiprobable at all intervals since the last shock. This variable schedule should leave the time after shock associatively neutral in the control groups since there are no consistent relationships between time after shock and the next shock. In the summation test suppression to a compound of an excitor (a tone) and the presumed inhibitor (time after shock) were compared to suppression to the excitor alone. In the retardation test the presumed inhibitor (time after shock) was paired with shocks to determine whether inhibitory training to time after shock would retard acquisition of excitatory strength to time after shock.

Method

Subjects

The subjects were 32 male albino rats 75-80 days old on arrival from Camm Research Lab, N.J. They were maintained at 80% of free feeding body weight throughout experimentation.

Apparatus

Eight Skinner boxes with grid floors, centrally mounted levers, and left-side dipper feeders were housed in ventilated .61-m cubes of 12.7 mm plywood lined with acoustical tile. The CS was a 1000-Hz 84-dB (re 20 $\mu N/m^2$) tone presented through a 10-cm speaker on the lid of each chamber. Scrambled grid shock USs were provided by Grason-Stadler shock sources (Model E10646S and 700). Barpressing, the baseline response to be suppressed by CS trials, was reinforced with 4-sec presentations of a .1-cc dipper cup containing a 32% (w/w) sucrose solution. The chambers were lit by a 28-V cue light mounted over the dipper opening 95 mm above the grid floor and by another 28-V bulb mounted on the outside of the right hand clear plastic wall.

Procedure

<u>Preliminary training</u>. All rats were magazine trained and shaped to barpress for 32% sucrose (w/w). Every barpress was reinforced, and every rat earned 90 reinforcements in each of four sessions. In the next four sessions, barpressing was reinforced on a VI 1-min schedule (Fleshler & Hoffman, 1962). These sessions and all the remaining ones unless otherwise noted were 32-min long.

<u>Experimental treatment</u>. On the day following the last preliminary training day the rats were divided into four groups of eight each. Each day two groups, RE (Retardation-experimental) and RC (Retardation-control), received six tone-shock pairings while barpressing for food on the VI schedule. The 1-min tone and 1-sec shock were coterminus. For Group RE the intershock interval was a constant 5 min and was designed to make time after shock inhibtiory. For Group RC the intershock interval was variable (81 to 730 sec) with a mean of 5 min and was designed to leave time after shock associatively neutral. Two more groups, SE (Summation-experimental) and SC (Summation-control), received treatments identical to Groups RE and RC respectively. For the first five sessions the shock intensity was .5 mA. For the next two sessions it was .8 mA; and for the last two sessions

it was 1 mA.

Recovery. On the day following the last day of experimental treatment, all rats in Groups RE and RC were run for 2 days on the VI 1-min baseline with no stimulus presentations. All rats in Groups SC and SE were run on the VI 1-min baseline for one session. One rat in Group SC and one in Group SE were given an extra session immediately following the first because their total responding was low (less than 25% of their total responding on the last day of preliminary training.)

Retardation test. On the day following the last recovery day, Groups RE and RC were tested for acquisition of suppression to time after shock. During each of four daily sessions, each rat received four pairs of shocks. Each pair consisted of a shock followed after 30 sec by a second shock. Thus, the time after the 1st shock was paired with a 2nd shock. If time after shock was inhibitory in Group RE then the suppression to the 2nd shock should not be as great as it is in Group RC. All shocks were 1-mA in intensity and 1-sec in duration. Each session was 24.5 min in length. Excitation following either shock in a pair was indexed by the use of a ratio, $D/(D+B)$, in which D was the number of responses in the 30 sec following one of the shocks and B the number of responses in the 30 sec before the first shock of the pair.

Two animals from Group RC were lost after 2 days of testing for reasons unrelated to the experiment.

Summation test. On the day following the recovery day, Groups SC and SE were tested for suppression to a compound of tone and time after shock. Both groups received two presentations of shock-tone pairings and two presentations of tone alone. Shock offset and tone onset were simultaneous for the pairings. Testing lasted for 2 days. Half the rats from each group received the compound and tone-alone presentations in an ABBA sequence, the other half in a BAAB sequence. The sequences were reversed on the 2nd day. Excitation was indexed by the use of a ratio, $D/(D+B)$, in which D was the number of responses during the 1-min tone and B the number of responses in the 1-min period prior to the shock for the pairings or prior to the tone for tone-alone trials.

Results

Retardation test. Over the four days of retardation testing pre-CS rates averaged 8.5 responses per minute for Group RE and 7.7 responses per minute for Group RC. Wilcoxon rank sum tests conducted separately on each day showed no group differences in pre-CS rates (p's>.05). Median suppression ratios for each group are shown in Table 1. SR_1 refers to suppression during the 30 sec following the first shock of a pair. SR_2 refers to

Table 1

Median suppression in the retardation test of Experiment 1

Group	Day 1	2	3	4
	SR_1			
RE	.57	.57	.65	.56
RC	.49	.39	.36[a]	.37[a]
	SR_2			
RE	.57	.52	.56	.55
RC	.40	.31	.48[a]	.24[a]

[a] $\underline{n} = 6$

suppression during the 30 sec following the second shock of a pair. Two-tailed Wilcoxon rank sum tests conducted separately over the four test days indicated a significant groups effect on each day for both the SR_1 ($W(8,8)=87$, $W(8,8)=92.5$, $W(6,8)=69$, $W(6,8)=68$, p's $< .05$)[1] and the SR_2 measure ($W(8,8)=94$, $W(8,8)=88$, $W(6,8)=68$, $W(6,8)=73$, p's $< .05$). Group RE was found to suppress less than Group RC during the interval between pairs of shocks and also during the 30 sec following the second shock.

<u>Summation</u> <u>test</u>. Since in a summation test we are primarily concerned with whether an animal responds more during the compound than during the single stimulus presentations, comparisons were made between each animal's suppression on a shock-tone trial and an adjacent tone-alone trial. The median difference in suppression to the compound and the tone-alone are given for each group in Table 2. A one-tailed Wilcoxon signed ranks test was used to evaluate the results. Calculated over both days of testing, the pre-shock significantly weakened suppression to the tone in both the experimental ($T^* = 1.804$, $p < .05$) and the control groups ($T^* = 3.27$, $p < .01$). On the 1st day of testing, a significant difference was found for the control group ($T+ = 98.5$, $p < .04$, $N=15$) but not for the experimental group ($T+ = 78.5$, $p > .05$, $N=16$). On the 2nd day of testing, suppression to the

Table 2

Median difference in suppression to the compound and tone-alone in the summation test of Experiment 1

Group	Day 1	Day 2
SE	.07	.09
SC	.03	.07

Note. A difference score is defined as the suppression ratio of a compound trial minus the suppression ratio of an adjacent tone-alone trial.

compound was significantly less than suppression to the tone for both the control group ($T+ = 114$, $p < .01$, $N=16$) and experimental group ($T+ = 106.5$, $p < .025$, $N=16$). Between-group comparisons of the difference scores were made using a one-tailed Wilcoxon rank sums test. These comparisons were appropriate for demonstrating differences in the relative magnitude of the summation effects because the two groups did not differ in suppression to the tone on the last conditioning day ($W(8,8) = 59$, $p > .05$). There were no significant differences between the experimental and control groups in difference scores on the 1st day ($W(8,8) = 57$, $p > .05$), the 2nd day ($W(8,8) = 57.5$, $p > .05$), or both days combined ($W(16,16) = 220$, $p > .05$).

Discussion

In the retardation test, time after shock in the experimental group was found to control less excitatory strength than time after shock in the control group despite being paired with the same shocks. This result in a retardation test indicates that the stimulus in the experimental group is inhibitory or that the experimental animals are not attending to the stimulus, and thus, will not acquire excitatory strength to that stimulus as quickly as they would to a more salient stimulus. The summation test results, however, argue against the lack-of-attention explanation of the retardation test findings. If the experimental animals were not attending to the stimulus (time after shock), then there should have been no difference between suppression to the tone-alone and the compound of tone and time after shock. But, in the summation test, Group SE was found to suppress less to the compound of tone and time after shock than to tone-alone, indicating that the experimental animals were indeed attending to time after shock.

The results discussed so far have supported the hypothesis that the temporal stimuli following shock (and explicitly unpaired with shock) do in fact become inhibitory. As expected from the hypothesis, Group RE was retarded relative to Group RC; and, in Group SE, the temporal stimuli, again as expected, reduced suppression to a known excitor when the two were compounded. However, it was also expected that the temporal stimuli would reduce suppression to the excitor more for Group SE than for Group SC. This result was not obtained. The failure to obtain this finding, however, does not demand rejection of the conclusion that the temporal stimuli become inhibitory. It may be that the summation test was not as sensitive to inhibitory effects as was the retardation test (cf. Baker, 1977; Witcher & Ayres, in preparation) and that some inhibition was conditioned to the temporal cues in Group SC even though this was not intended. One difficulty in finding the hypothesized difference between Groups SE and SC could be an insensitivity of the summation test at the level of suppression of the excitor. In order to see a summation effect in a compound it is necessary that the excitatory stimulus be sufficiently strong for the additive effect to be evidenced. Since mean suppression (averaged over all rats) to the tone on the last conditioning day was .25, it may have been too weak for the complete detection of summation effects.

Another factor that may have attenuated the expected difference in inhibitory summation between Groups SE and SC could be the duration of the CS. Suppression ratios were formed using the number of responses recorded during the 1-min CS for both tone-alone and shock-tone trials. But responding may vary over time. A closer examination of the data from the experimental rats shows a nonsignificant increase in responding from the first 30 sec of the CS to the second 30 sec (Sign test, $p = .061$) on the last conditioning day. Also there was a significant decrease (Sign test, $p = .012$) in responding from the first to the second half of the minute following the shock. This suggests that possible strong summation effects in the first half of the compound trial may be washed out by weaker summation effects in the second half minute.

A third possible explanation for the lack of a hypothesized difference between Groups SE and SC may be that the control procedure did not properly control for the variable for which it was intended. The control procedure in this study was designed to eliminate the predictability of the duration of the intershock interval. A schedule of shock presentations was devised (Fleshler & Hoffman, 1962) to make the probability of a US equiprobable over time. But a problem with this procedure is that the theoretical equiprobability can only be approximated in practice. The rat is exposed to a schedule in which shocks are not equiprobable at all times, and thus, may come to be controlled by subtle temporal relationships. In the schedules used in this study, the rats were exposed to shocks that were separated by at least 2 min four-fifths of the time. It is possible that the rats in Group SC were controlled by these scheduled relationships of relatively shock-free post-shock periods. Thus inhibitory strength may have accrued to the post-shock periods making this control procedure a conservative one.

Experiment 2

The results of Experiment 1 suggested that time after shock became inhibitory in the experimental groups. The failure to find group differences in the summation test, however, was not expected. It was argued in the discussion of Experiment 1 that the failure to find the predicted differences could be due to procedural problems. In Experiment 2 a second summation test was given. Two groups of rats were given treatment similar to that given to Groups SE and SC in Experiment 1 except for certain manipulations designed to increase conditioning to the tone and to enhance between-group differences in the final summation test. Specifically the shock intensity was set at a high level from the beginning of conditioning to increase excitation to the tone; a shorter CS period was used to prevent strong inhibition immediately after shock from being obscured by weaker inhibition in the 2nd half of a long CS; and a longer intershock interval was used to increase inhibitory strength to time after shock in Group SE making the shock-free period after shock longer.

Davis (1970) suggested a non-associative explanation of post-shock bursts of responding in conditioned suppression experiments that use a VI schedule of reinforcement.

He pointed out that with a VI schedule an animal's suppression to the CS would increase the probability of reinforcement for a post-shock response. With training, presumably the animal should come to be controlled by this contingency, and post-shock responding should increase. To test this suggestion, a third group was run in a manner similar to Group SE except that conditioning took place off the baseline. Thus these animals were not exposed to a contingency in which a response after suppression to the CS led to reinforcement, and therefore, they should not according to Davis' suggestion exhibit post-shock bursts of responding when tested on the baseline.

Method

Subjects and Apparatus

The subjects were 24 male albino rats 80-85 days old on arrival from Holtzman Co., Madison, Wisc. They were maintained at 80% of free feeding body weight throughout experimentation. The apparatus was that described in Experiment 1.

Procedure

Preliminary training. All rats were magazine trained and shaped to barpress for 32% sucrose (w/w). Every barpress was reinforced, and every rat earned

90 reinforcements in each of four sessions. In the next four sessions, barpressing was reinforced on a VI 1-min schedule (Fleshler & Hoffman, 1962). These sessions and all the remaining ones were 26 min in duration.

Experimental treatment. On the day following the last preliminary training day, the rats were divided into three groups of eight each. Two groups, CT (constant-tone), and VT (variable-tone), received four tone-shock pairings per day on the VI baseline. The 30-sec tone and 1-sec 1-mA shock were coterminous. For Group CT the intershock interval was a constant 6 min. For Group VT the intershock interval was variable (49 to 859 sec) with a mean of 6 min. The third group, OCT (off-the-baseline-constant-tone), received treatment identical to Group CT except that the VI schedule of reinforcement was not in effect and the bar was removed from the cage. All groups received six daily sessions of experimental treatment.

Recovery. Each rat was placed in the chamber for three daily sessions under the VI 1-min schedule of reinforcement.

Testing. On the day following the last recovery day Groups CT, VT, and OCT were tested for suppression to a compound of tone and time after shock. All groups received a presentation of a tone and a shock-tone pairing. Shock offset and tone onset were simultaneous for the pairings. Testing lasted for 3 days. Excitation was indexed by a suppression ratio, $\underline{D}/(\underline{D}+\underline{B})$, in which $\underline{D}$ was the number of responses during the tone and $\underline{B}$ was the number of responses in the 30 sec prior to the tone for the tone-alone trials or prior to the shock for shock-tone pairings.

Results

Median suppression ratios for each day for each group are shown in Table 3. Between-group comparisons were made using difference scores calculated for each rat by subtracting the suppression ratio for the tone-alone trial from the suppression ratio for the compound trial. A one-tailed Wilcoxon rank sum test was used to test between-group differences. A one-tailed Wilcoxon signed ranks test was used to test within-group differences. Difference scores in which one of the pairs of ratios was 0/0 were not included in the analyses. Analysis of the 1st test day's data showed that the pre-shock significantly weakened suppression to the tone in Group CT ($T+ = 14$, $\underline{p} < .05$, $N=5$) and in Group OCT ($T+ = 15$, $\underline{p} < .05$, $N=5$) but not in Group VT ($T+ = 6$, $\underline{p} > .05$, $N=6$). Also the amount of reduction in suppression was found to be significantly greater in Group CT than in Group VT ($W(5,6) = 40.5$, $\underline{p} < .05$)

Table 3

Median suppression to the compound and to the tone in the summation test in Experiment 2

Group	Day 1 Tone	Day 1 Compound	Day 2 Tone	Day 2 Compound
CT	.00	.67	.00	.20
VT	.00	.00	.00	.15
OCT	.00	.40	.40	.37

and in Group OCT compared to Group VT ($W(5,6) = 40$, $p < .05$). There were no differences between Groups CT and OCT in amount of suppression reduction ($W(5,5) = 27$, $p > .05$). On day 2 there were no between-group differences in the amount of reduction of suppression.

Discussion

The summation test results of Experiment 2 along with the retardation test results of Experiment 1 demonstrate according to accepted criteria (Rescorla, 1969) the inhibitory nature of time after shock. At the same time the results rule out suggested non-associative accounts of post-shock responding. Shock-elicited responding explanations are inconsistent with the obtained differences between the experimental and control groups. For if responding was shock-elicited, then suppression should have been approximately the same in all groups since they all had received equal numbers of shock. But the results showed that the experimental groups did not suppress as much as the control groups in both the retardation test of Experiment 1 and in the compound trials of the summation test of Experiment 2. The results of the summation test of Group OCT of Experiment 2 argues against an explanation of post-shock responding in terms of a learned contingency between suppression to the CS and probability of reinforcement after the CS. The rats in this group received conditioning off the baseline. Thus they had no opportunity to learn that there was an increased liklihood of reinforcement for a response after suppression to the CS. The rats still showed strong summation effects, demonstrating the relative unimportance of this contingency in post-shock responding.

The development of conditioned inhibition to discrete stimuli following shock has been explained in a variety of ways (cf. Maier, Rapaport, & Wheatley, 1976). Relaxation theory (Denny, 1971) and opponent-process theory (Solomon and Corbit, 1974) have similar accounts of the development in that both postulate a positive afterreaction to an aversive stimulus that reflects itself in reduced suppression in a conditioned suppression procedure. Both theories postulate that the afterreaction follows a time course in which it reaches a maximum soon after the offset of the aversive stimulus and then slowly dissipates over time. Also the two theories predict that a stimulus paired with this afterreaction will come to control the same reduced suppression. Thus the two theories have an associative account of increased responding during a post-shock discrete stimulus but a postulated non-associative account for increased responding during time after shock. These non-associative accounts suffer from the same difficulties as other non-associative accounts in dealing with the results of Experiments 1 and 2. That is, if the strength of the afterreaction depends only on the number and intensity of the aversive stimuli, then there should be no difference in responding following the experimental and the control procedures. These theories with modification can however account for the present results. Both theories postulate that initially the time course of the afterreaction is not well-defined but that over trials it becomes better defined. The process that leads to this increased definition is only postulated and not explained. The time course, though, can be predicted without postulation. Assuming only that an afterreaction does occur following a shock and that it dissipates slowly, temporal conditioning can account for the development of a specific time course. That is, initially the afterreaction would be evidenced in all intervals following shock, and over trials it would become conditioned to all temporal stimuli following shock. If, however, some of the intervals are also paired with excitatory processes, then the inhibition conditioned to those intervals should be weakened. For the experimental groups no excitatory process occurred closer than 4 min after the last US. For the control groups an excitatory process followed the

US by less than 4 min on many occasions. Thus the acquisition of an association between the inhibitory afterreaction and temporal cues should have been weaker in the control group relative to the experimental group.

Contingency theory (Rescorla, 1969) and the Rescorla-Wagner (1972) model could account for conditioned inhibition to time after shock in the same way they account for conditioned inhibition to a discrete stimulus presented after shock. Contingency theory predicts that a stimulus that is explicitly unpaired with shock will become inhibitory. Time after shock (with a sufficiently long intershock interval) is unpaired with shock, and thus, should become inhibitory. The temporal stimuli should become more inhibitory for the experimental groups than for the control groups because the time immediately after shock was never explicitly paired with shock in the experimental procedure but was occasionally paired with shock in the control procedure. The Rescorla-Wagner model predicts that a stimulus will become inhibitory when that stimulus is presented unreinforced in compound with an excitatory stimulus. In Experiments 1 and 2 the temporal stimuli following shock were unreinforced in the presence of background cues made excitatory by the shocks.

Experiments 1 and 2 do not distinguish between the associative accounts of conditioned inhibition to time after the US. They also do not get at the question of what aspects of time after shock are the effective stimuli controlling the animal. The experiments do show however that temporal stimuli can function as inhibitory stimuli in the same way as do discrete stimuli. In Experiment 3 the functional nature of temporal stimuli will be explored with another classical conditioning phenomenon, blocking.

Experiment 3

Blocking is a term used by Kamin (1969) to refer to the results of a procedure in which two stimuli are reinforced in compound following prior treatment in which one of the stimuli has already been conditioned. Typically, following such a procedure, the stimulus that was not pretreated is found to have little or no associative strength conditioned to it. The pretreated stimulus is said to have "blocked" conditioning to the nonpretreated stimulus. Evidence for this result was found using a variety of procedures and stimuli (cf. Kamin, 1969; and Mackintosh, 1971). Suiter and LoLordo (1971) found also that prior inhibitory training to one stimulus can block inhibition from accruing to a second stimulus trained in compound with the first. Kamin's (1969) surprisal notion and Rescorla and Wagner's model of conditioning predict these results. But the empirical and theoretical evidence for blocking refers to procedures involving discrete CSs. In this experiment excitatory and inhibitory blocking of a discrete CS by a temporal cue was attempted. Excitatory blocking of a discrete CS (tone) by a temporal cue (time before shock) was attempted by reinforcing a compound of the tone and pretreated time before shock. The pretreatment of time before shock consisted of shock-alone presentations with a constant intershock interval. This pretreatment should make this time before shock excitatory since it is consistently paired with shock. A control group received identical treatment except that during pretreatment the shocks were presented with a variable intershock interval. Thus, time before shock was not paired consistently with shock and should not become excitatory and block conditioning to the tone during compound training. Inhibitory blocking of a discrete CS (tone) by a temporal cue (time after shock) was attempted by reinforcing a compound of the tone and pretreated time after shock. The pretreatment of time after shock consisted of shock-alone presentations with a constant intershock interval. This treatment should make the time after shock inhibitory as demonstrated in Experiments 1 and 2. A control group received identical treatment except that during pretreatment the shocks were given with a variable intershock interval. Thus, time after shock was not paired consistently with shock or shock-free periods and should not become inhibitory and block inhibitory conditioning to the tone during compound training.

Method

Subjects and Apparatus

The subjects were 32 male albino rats 80-85 days old on arrival from Holtzman Co., Madison, Wisc. They were maintained at 80% of free feeding body weight throughout experimentation. The apparatus was that of Experiment 1.

Procedure

Preliminary training. Barpress training was unchanged from Experiment 2 except that sessions were 33 min in duration.

Pretreatment. On the day following the last preliminary training day, the rats were divided into four groups of eight each. For the next 18 sessions all groups received eight 1-sec 1-mA shocks per daily session. Groups FB (forward-block) and BB (backward-block) received the shocks with a constant intershock interval of 4 min. This pretreatment was designed to make time before shock excitatory for Group FB and time after shock inhibitory for Group BB. Groups FC (forward-control) and BC (backward-control) received the shocks with a variable intershock interval averaging 4 min. This pretreatment was designed to leave time before shock and time after shock associatively neutral in Groups FC and BC.

Compound conditioning. On the day following the last day of shock-alone treatment, Groups FB and FC in each of four daily sessions received eight tone-shock presentations. The tone was 1 min in duration. The tone and shock coterminated. The intershock interval was 4 min. Thus, a tone-shock presentation was a compound of the tone and an excitatory temporal cue (the 60 sec before shock). Groups BB and BC received identical treatment except that the tone began as the shock terminated. Thus, these groups received presentations of a compound of tone and an inhibitory temporal cue (the 60 sec after shock).

Recovery. All groups were given 2 daily sessions in which no stimulus presentations were made and the rats were allowed to barpress for food on the VI 1-min schedule of reinforcement.

Testing. Groups FB and FC received 4 days of testing in which they were presented with a single CS during the 16th min of the session. Groups BB and BC received 3 days of testing during which they were presented with a single CS-US pairing during minute 11.

Results and Discussion

Backward groups

Mean suppression to the tone is shown in Figure 2 for each group during compound conditioning and testing. The data was analyzed using two-tailed Wilcoxon rank sum tests to detect between-group differences and two-tailed Wilcoxon signed rank tests to detect within-group differences. Analysis showed no evidence of blocking during retardation testing (p's $> .05$). That is, Group BB did not differ from Group BC in suppression to the tone. Also the suppression to the tone did not increase over days for either group (p's $> .05$). A comparison of each animal's suppression to the tone with its suppression in the minute after the shock showed that the rats in both groups suppressed less to the tone (p's $< .05$). Since time after shock was shown in Experiments 1 and 2 to be inhibitory, this suggests that the tone was inhibitory for both groups.

Forward groups

Mean suppression to the tone for each group during compound conditioning and testing is shown in Figure 3. Analysis of the compound conditioning data showed no effect of groups on any day (p's $> .05$). Also suppression did not increase over days (p's $> .05$). The lack of an effect of days would seem to indicate that no conditioning had taken place during the compound conditioning phase. The test data showed however that the tone was excitatory for both groups. The failure to see an increase in suppression across compound conditioning sessions may have been due to the relatively low response rates. On average the rats of both groups responded at an overall rate that was 36% of the rate they had exhibited over the last 2 days of VI training. These low rates may have obscured conditioning by increasing the variability of suppression ratios. The low rates probably reflected suppression to background cues made excitatory by the unsignalled shocks in the pretreatment phase. Following the recovery sessions the animals responded at an overall rate that was on average 77% of their rate over the last 2 days of VI training. These high response rates make the suppression ratio measure less variable. Thus, the dramatic increase in suppression from the last compound conditioning trial to the first test trial probably did not represent a change in the absolute excitatory strength of the tone but rather a change in the sensitivity of the suppression ratio measure at various levels of the operant baseline. Analysis of the test data showed no group effects (p's $>$ .05). But since it was demonstrated in Experiment 1 that with long duration CSs temporal effects could be masked, the test data were examined further. New suppression ratios were formed reflecting suppression for each 30 sec of the 60 sec tone. Mean suppression for each 30 sec for each group during testing is depicted in Figure 4. Analyses conducted on the results separately or combined over the 3 test days found no significant differences between groups in suppression to the first 30 sec of the tone (p's $> .05$). A similar analysis of the suppression in the second 30 sec of the tone did show a groups effect ($W^* = 2.46$, $p < .05$) when the data was combined but not when done separately over days (p's $> .05$). The blocking group was found to have suppressed more than the control group.

The finding of greater suppression in the second 30 sec of the tone in the experimental group indicates that the experimental procedure had an effect. The effect, though, is in the opposite direction from what was predicted. If prior conditioning to time had blocked conditioning to the tone, then the experimental group should have suppressed less to the tone than should the control group. The results show that the effect of the prior conditioning to time had its effect not on overall suppression to the tone but rather on the pattern of suppression during the tone. The results indicate that in the experimental group suppression was controlled not only by the tone but also by the time to the US, while in the control group suppression was controlled only by the tone. The pattern shown by the experimental animals of increasing excitation over the duration of a CS has been noted before (Pavlov, 1927; Estes & Skinner, 1941; Millenson & Hendry, 1967). Pavlov (1927) has referred to the phenomenon as "inhibition of delay". Others (Millenson & Hendry, 1967; Sheffield, 1965) prefer to describe the phenomenon in terms of a temporal discrimination. These authors suggest that initially an animal will respond to all parts of the CS due to stimulus generalization. Later the animal will form a discrimination between the initial portion of the CS which is never paired with the US and later portions of the CS which are always closely paired with the US. The experimental manipulation of this study (the presentation of shocks with a constant intershock interval) has apparently not blocked conditioning but instead facilitated the learning of this temporal discrimination. That is, after being controlled by temporal cues associated with one prior signal (the US that occurred 4 min before the following US), the experimental animals were more readily controlled by temporal cues (CS onset) associated with another signal (the CS). So instead of blocking, what has occurred is transfer of training.

The results of this experiment are not necessarily inconsistent with some of the major theoretical accounts of the blocking phenomenon. Kamin (1969) suggested that the crucial aspect of the blocking experiment was the redundacy of the added stimulus. If the added stimulus was not redundant, then blocking would not occur. In this study, although a shock is already predicted by the time since the last shock, the addition of the tone is probably not redundant. Rats do not exhibit perfect temporal discrimination. Thus, an event (tone onset) which occurs only 1 min before the US is, for the rat, a better predictor of the US than an event (a previous shock) which occurs 4 min before the US. As a better predictor, the added tone would not be redundant, and so, conditioning to the tone should not be blocked.

The Rescorla-Wagner model predicts blocking when the pretreated stimulus has accrued to it all the excitatory strength tenable by the US. Thus during compound conditioning there is not enough excitatory strength available to accrue to the added stimulus. According to this model, blocking will not occur whenever the pre-treated stimulus has not accrued to it available excitatory strength or when the relative salience of the new stimulus is high. Although no measures of relative salience were made in this study, it is not unlikely that the salience of the temporal cues associated with the 4-min intershock intervals were not as salient as the tone. Thus the tone could successfully compete for excitatory strength and blocking would not occur.

General Discussion

These experiments were an attempt to understand the functional nature of temporal cues in two Pavlovian conditioning procedures, inhibition training and blocking. Experiments 1 and 2 have demonstrated that the temporal cues after shock can come to control inhibitory strength in the same way as discrete cues. The failure to find a difference in inhibitory summation between experimental and control groups in Experiment 1 suggests, however, that inhibition with temporal cues is difficult to demonstrate. One difficulty is in designing a proper control procedure. A frequently used control procedure is the truly random control (Rescorla, 1967). The truly random procedure requires that the CS and US be distributed randomly and independently of each other. Time after shock by definition cannot be presented independent of shock, and therefore, a truly random control cannot be used. The variable intershock interval schedule of US presentations, used in this study as a control procedure, had the advantage of making shocks unpredictable but had the disadvantage of making shock-free periods fairly predictable. That is, time after shock was generally shock-free for short periods of time. Thus, this control procedure is a conservative one. Another difficulty in demonstrating inhbition is in defining the effective stimulus. Time after shock has been arbitrarily defined in this study as either the 30 sec or 1 min following shock. Inhibitory summation was shown with the 30 sec duration but not with the 1 min duration. It is not possible with the present data to decide for what period the temporal cues after shock are inhibitory. Parametric studies, in which the duration of the added stimulus is systematically varied, may help bound the period that controls inhibition; but poor sensitivity (Baker, 1977; Witcher & Ayres, in preparation) of the summation test and the conservative nature of the control procedure would make this difficult.

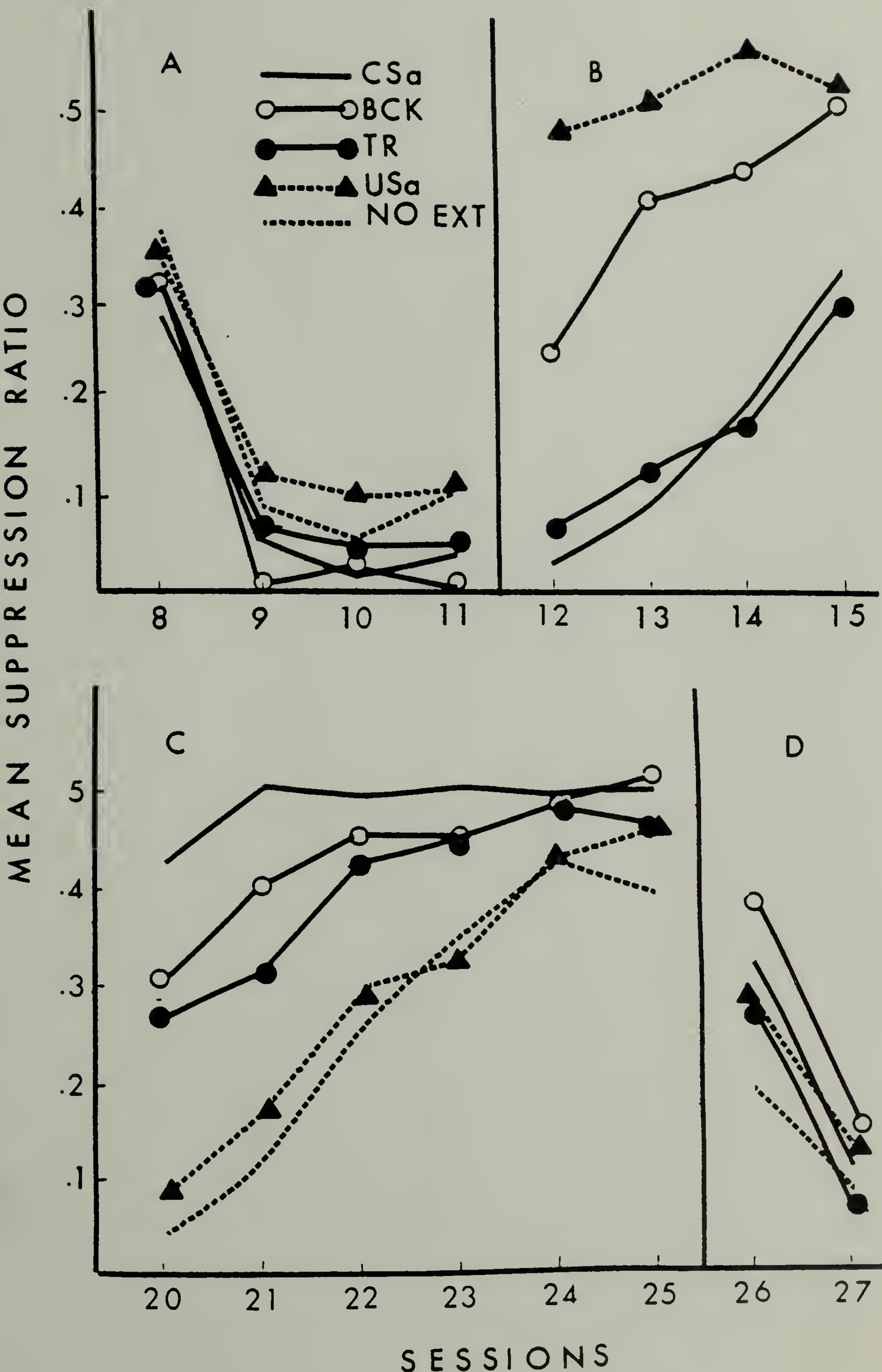
Experiment 3 has failed to find blocking of conditioning to discrete cues by temporal cues that precede or follow shock. While the failure to obtain blocking may have been due to a special nature of temporal cues, it was suggested that the failure arose from characteristics of temporal cues that if found in discrete cues would also lead to a failure in blocking. Specifically, it was suggested that blocking did not occur because of the relatively low salience of temporal cues and the increased predictiveness of the discrete cue as a signal. Both salience and predictiveness have been shown to be important variables in obtaining blocking with discrete cues (cf. Mackintosh, 1974).

The results of the experiments above have shown that the functional nature of temporal cues with respect to inhibition and blocking is similar to that of discrete cues and consistent with major Pavlovian theoretical formulations. Further research is needed in order to extend the similarities of discover differences.

Footnotes

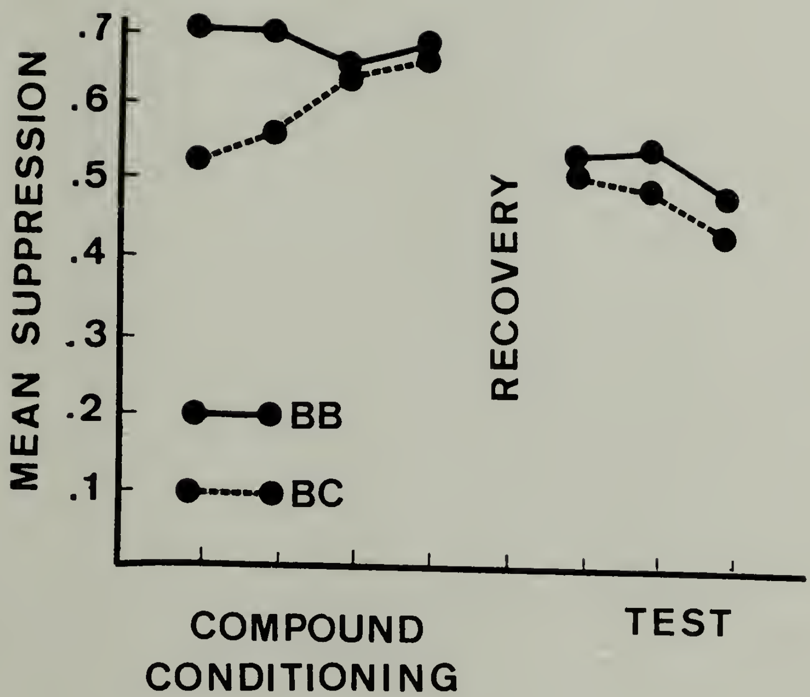
[1]All notation for non-parametric statistics used in this study follows that of Hollander & Wolfe (1973).

Figure 1. Conditioned suppression in Experiment 2 during (A) forward conditioning, (B) experimental treatment, (C) CS-alone testing, and (D) reacquisition. Sessions are numbered consecutively for the entire experiment. The first forward conditioning session (Session 8) was preceded by 3 shaping and 4 VI-training sessions. Sessions 16 through 19 were VI sessions without CSs or USs. (From Ayres et al., 1976)



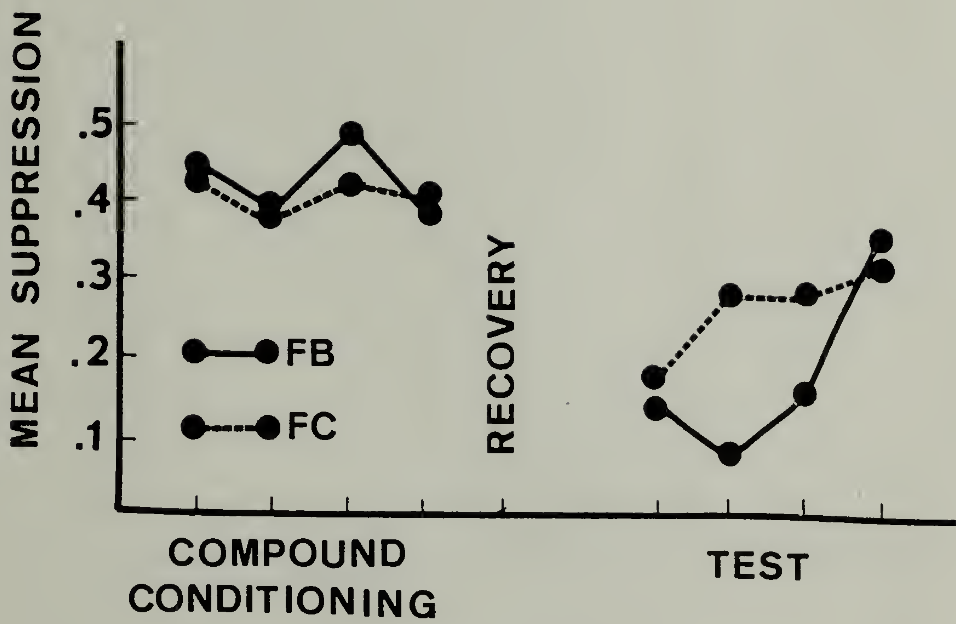
A
B
C
D
CSa
BCK
TR
USa
NO EXT
MEAN SUPPRESSION RATIO
SESSIONS

Figure 2. Mean suppression to the tone for Groups BB and BC during compound conditioning and testing in Experiment 3.



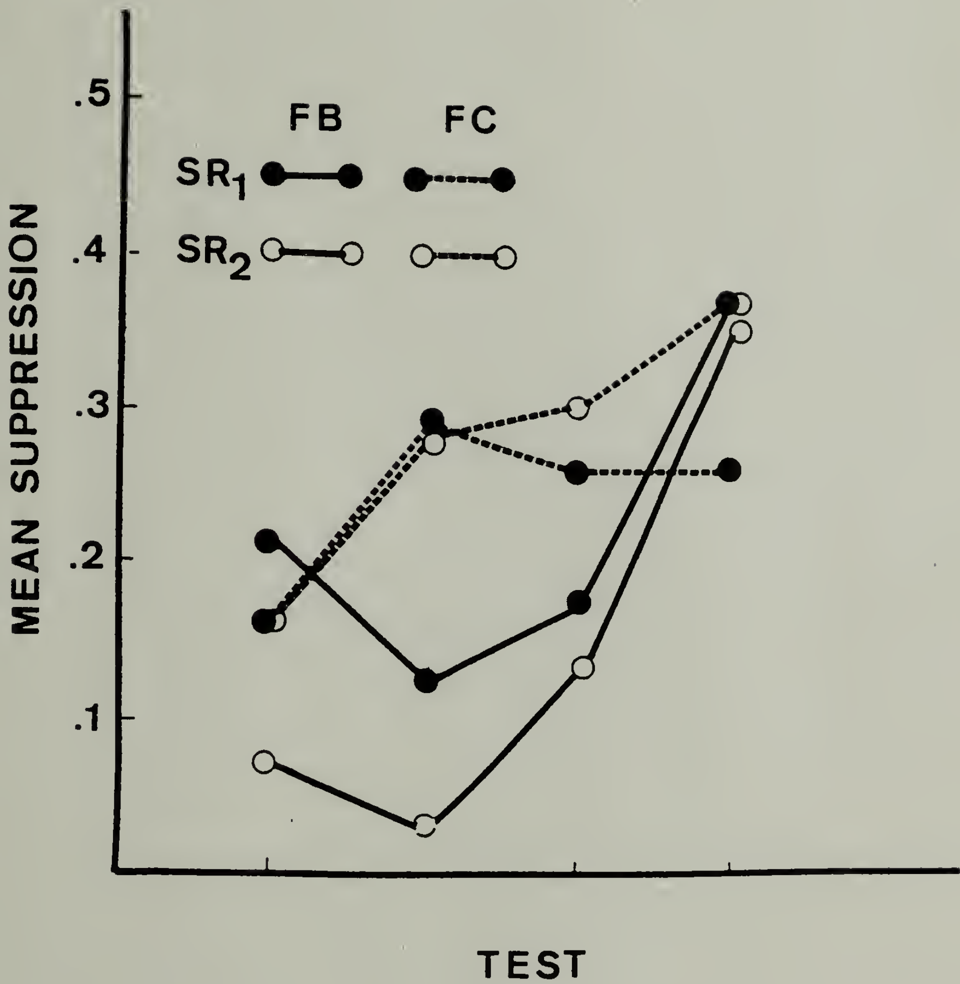
MEAN SUPPRESSION
.7
.6
.5
.4
.3
.2
.1
BB
BC
RECOVERY
COMPOUND
CONDITIONING
TEST

Figure 3. Mean suppression to the tone for Groups FB and FC during compound conditioning and testing in Experiment 3.



MEAN SUPPRESSION
.5
.4
.3
.2
.1
FB
FC
RECOVERY
COMPOUND
CONDITIONING
TEST

Figure 4. Mean suppression for each 30 sec for Group FB and FC during testing in Experiment 3. SR_1 refers to suppression calculated on the first 30 sec of the tone. SR_2 refers to suppression calculated on the second 30 sec of the tone.


.5
.4
.3
.2
.1
MEAN SUPPRESSION
FB
FC
SR_1
SR_2
TEST

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